Chironomidae larvae (Diptera) of Neotropical floodplain: overlap niche in different habitats

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Abstract

The niche overlap between trophic groups of Chironomidae larvae in different habitats was observed between trophic groups and between different environments in Neotropical floodplain. For the evaluation we used the index of niche overlap (C_{XY}) and analysis of trophic networks, both from the types and amount of food items identified in the larval alimentary canal. In all environments, the larvae fed on mainly organic matter such as plants fragments and algae, but there were many omnivore larvae. Species that have high values of food items occurred in diverse environments as generalists with great overlap niche and those with a low amount of food items with less overlap niche were classified as specialists. The largest number of trophic niche overlap was observed among collector-gatherers in connected floodplain lakes. The lower values of index niche overlap were predators. The similarity in the diet of different taxa in the same niche does not necessarily imply competition between them, but coexistence when the food resource is not scarce in the environment even in partially overlapping niches.

Keywords: aquatic invertebrate, food recourses, food webs, lakes, Upper Paraná River.

Larvas de Chironomidae (Diptera) de uma planície de inundação neotropical: sobreposição de nichos em diferentes habitats

Resumo

A sobreposição de nichos entre grupos tróficos de larvas de Chironomidae em diferentes tipos de ambientes foi verificada entre os grupos tróficos e entre diferentes ambientes em uma planície de inundação Neotropical. Para a avaliação foi utilizado o Índice de Sobreposição de Nicho (C_{XY}) e análises de redes tróficas, ambos a partir dos tipos e quantidade de itens alimentares identificados no tubo digestivo das larvas. As larvas alimentaram-se em todos os ambientes principalmente de detritos orgânicos como os fragmentos de plantas e algas, porém, verificou-se alto nível de omnívora. As espécies que tem altos valores de itens alimentares ocorreram em diversos ambientes como generalistas e com grande sobreposição de nichos e aqueles com baixos itens alimentares e com menor sobreposição foram classificados como especialistas. O maior número de sobreposição de nichos tróficos foi verificado em coletores-catadores nas lagoas com conexão. Os menores valores do índice foram verificados nos predadores. A semelhança na dieta de diferentes táxons e grupos tróficos em um mesmo nicho não implica, necessariamente, uma competição entre eles, porém uma coexistência quando o recurso alimentar não é escasso no ambiente, mesmo com sobreposição parcial de nichos.

Palavras-chave: invertebrados aquáticos, recursos alimentares, rede trófica, lagoas, Alto rio Paraná.

1. Introduction

The identification of the patterns and mechanisms of species occurrence have been controversial issues in community ecology (Weither and Keddy, 1999; Ulrich, 2004). Early studies showed the importance of simple deterministic rules based on forbidden species composition and reduced niche overlap in the structure of natural

communities (Diamond, 1975). However, interspecific competition could not be somehow sufficient to describe the abundance and the diversity of species. Other stochastic processes may be involved (Hubbel, 2001), suggesting the role of environmental variability in determining patterns of community composition (Ellwood et al., 2009). Patterns

and mechanisms of species occurrence, niche overlap and their interactions have been largely explored in the last years, taking advantage of network theory as a useful framework to represent the structure of many complex systems as aquatic environments (Proulx et al., 2005).

Larvae of Chironomidae live in different habitats without selecting the available resources, minimising intraspecific and interspecific interactions (Dole-Olivier et al., 2009) so they are strongly influenced by variations in the physical and trophic microhabitats. The spatial segregation between different species in habitats can lead to spatial overlap, determining a trend for spatial intraspecific competitive interactions (Schmid-Arraya and Schmid, 1995). The niche of species can be defined as the environmental conditions that allow this species to satisfy its minimum requirements, so that birth rate of a local population is equal to or greater than its death rate (Chase and Leibold, 2003).

The interactions of species may lead to trophic niche overlap, important to quantify how two or more species overlap in the use of food resources (Albertoni et al., 2003; Mokany et al., 2008). The competition between the larvae of Chironomidae can lead to a niche overlap and even limit species with similarity of niches.

Detritivorous Chironomidae larvae furniture are clearly governed by biotic and abiotic stochastic processes (Schmid, 1993). The abiotic conditions and food availability are important factors in determining how the organisms in aquatic environments can colonise different habitats or migrate to other locations.

Researchers have advanced functional classifications of species into groups with similar biological and ecological traits that are expected to respond consistently along specific environmental gradients (Poff et al., 2006). The use of food webs for understanding overlap remains a hot topic for research in ecology, but the lack of cohesion in the approaches used to study them still hinders the field (Bellisario et al., 2012).

The feed and type of food eaten by different species of Chironomidae larvae are studied for their interactions with the great diversity of food resources (Henriques-Oliveira et al., 2003) and the recognition of their importance to the energy flow in aquatic ecosystems (Dole-Olivier et al., 2009). The analysis of the gut content provides valuable information about how the Chironomidae larvae exploit food resources in their different habitats.

This study aimed to evaluate the niche Chironomidae species and the interactions between species using the same habitat by analysing their digestive content, and these determine whether or not there exists niche overlap between different trophic groups. We have as a hypothesis that floodplain lakes have more overlap niche channels, because these environments possess habitats with the same food resources, so contain similar trophic spaces.

2. Material and Methods

2.1. Study area

The Ivinhema River is one of the main tributaries of the Upper Paraná River floodplain and the study area is part of the plain of the lower Ivinhema River course, which has a large quantity of littoral lakes (Stevaux et al., 2004) and is relatively flat. It is influenced by two climate types, tropical and sub-tropical (Souza Filho and Stevaux, 2004). Samples were collected at ten stations (Figure 1): the main river - Ivinhema River, Ipoitã channel (secondary channel) connects the Ivinhema with Paraná rivers, connected floodplain lakes (Patos, Sumida, Finado Raimundo e Boca do Ipoitã) and unconnected floodplain lakes (Cervo, Jacaré, Zé do Paco e Ventura).

2.2. Sampling and laboratory procedures

In each station, three points were sampled along a transect section from one margin to another, including the central region. For each point three sediment samples were collected, with a modified Petersen grab (0.0189 m²), quarterly, from February 2000 to May 2001.

In the field, water was added to the samples, and the larvae gaseously "anesthetized" to prevent regurgitation of food. After approximately one hour, the sediment was washed using sieves of mesh size 2 mm, 1 mm and 0.2 mm. The organisms retained in the first meshes were screened and treated with 70% alcohol. The sediment in the last sieve was stored in polyethylene bottles containing 70% alcohol for subsequent screening in the laboratory.

Larvae were identified using a microscope and identification keys by Epler (1995), Coffman and Ferrington (1996) and Trivinho-Strixino (2011).

The content analysis was performed with larvae digestive systems mounted on slides under a microscope Olympus CH30 (magnification 100x magnification) and identification keys by Krammer and Lange-Bertalot (1986, 1991) were used for identification of algae. The food items were counted throughout digestive contents for subsequent calculation of niche overlap using the numerical method, by taking the average of the items analysed by the average number of individuals of the same taxa.

2.3. Statistical analysis

To quantify the degree to which two or more taxa overlap to obtain the same food items, we used the Schoener Index Overlay Niche (Schoener, 1974). We calculated average food items in the digestive contents of individuals of the same taxa for each sample (a, b, c). The niche overlap varies from 0.0 to 1.0, considering the value of 0.6 as the total overlap of niches. The overlap was calculated according to the formula proposed by Hurlbert (1978):

$$Cxy = 1 - 0.5 (\Sigma |Px_1 - Py_1|)$$

Where, (Px_i) is the numerical proportion of food type, i is the diet of species x, and (Py_i) is the numerical proportion of food type (i) in the diet of species (y). To calculate the overlap of taxa, we used the average abundance of food items in each habitat and month of sampling. The number of niche overlap among taxa and trophic groups of different groups was assessed by a one-way ANOVA (Analysis of Variance).

Henriques-Oliveira et al. (2003) categorised trophic groups of Chironomidae larvae as: facultative predators,

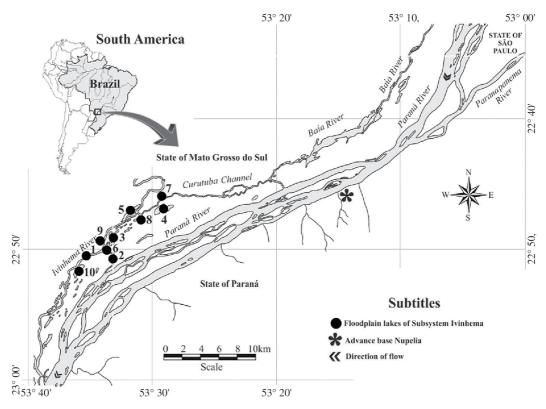


Figure 1. Location of study area and sampling stations. IR – Ivinhema River (1); IC - Ipoitã channel (2); PA - Patos floodplain lake (3); SU - Sumida floodplain lake (4); FR - Finado Raimundo floodplain lake (5); BI - Boca do Ipoitã floodplain lake (6); CE - Cervo floodplain lake (7); JA - Jacaré floodplain lake (8); ZP - Zé do Paco floodplain lake (9); VE - Ventura floodplain lake (10).

shredders herbivores, collector gatherers and collector filterers.

The graphs of trophics nets were plotted using the Program for Large Network Analysis - Pajek. Nestedness is a topological pattern in which interactions involving species with few connections represent a subset of the interactions involving highly-connected species (Bascompte et al., 2003; Bascompte and Jordano, 2007). We used the Aninhado 3.0 software to calculate the degree of nestedness with the metric Test T¹⁰ and NODF (program to calculate the nestedness in networks based on similar metrics), which varies from 0 to 100 (Almeida-Neto et al., 2008).

We normalised values so they ranged from 0 (nonnested) to 1 (perfectly nested). The significance of NODF was estimated with the Monte Carlo test procedure with 1,000 randomisations for both tests, using null model Ce, in which the interaction probability between Chironomidae morphotypes (30) and a food item (104) is proportional to their total number of interactions. The relative degree, the proportion of edges that relate to a vertex, considering a total of edges in the graph that could relate to it, was conducted to determine species with larger or smaller amplitudes in the diet.

Tests were made to find the differences in diet among the most common species using the Kruskal-Wallis test and this was also used to verify any feeding significance differences between the different environment types, stations and habitats.

The number of individuals of each species was selected for the analysis of digestive contents. A two-factor ANOVA was performed to test the differences among the averages of the index between months and sampling stations. We tested the differences in feeding and each taxon index values overlap in the types of environments, seasons and months of sampling.

3. Results

The mean values higher overlap index (> 0.6) were recorded in floodplain lakes of Patos and Sumida and lower values (< 0.2) were recorded in Jacaré and Zé do Paco floodplain lakes (Figure 2). The differences were highly significant by factorial ANOVA (F3, 72 = 6.21, p = 0.00) and the Kruskal-Wallis analysis (Figure 2).

Significant interactions occurred with complete overlap between all trophic groups, as debris and algae were the main items consumed by the majority. Considering the average values, the niche overlap was complete, especially among collector-gatherers and collector-filterers, and among collector-gatherers and shredder-herbivores (Table 1).

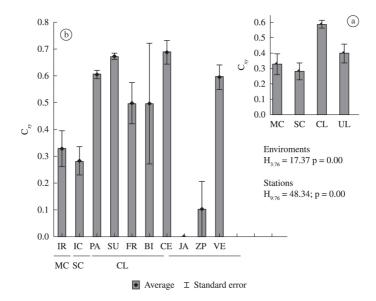


Figure 2. Mean values and standard error of the index of niche overlap (*Cxy*) among taxa in the four environments **MC**-main channel, **SC**- secundary channel, **CL**- connected lakes, **UL**- unconnected lakes (a) and the twelve sampling stations (b)- **IR** – Ivinhema River (*n*=151); **IC** – Ipoitã channel (*n*=169); **PA** – Patos floodplain lake (*n*=344); **SU** – Sumida floodplain lake (*n*=343); **FR** - Finado Raimundo floodplain lake (*n*=419); **BI** - Boca do Ipoitã floodplain lake (*n*=159); **CE** - Cervo floodplain lake (*n*=1481); **JA** - Jacaré floodplain lake (*n*=167); **ZP** - Zé do Paco floodplain lake (*n*=44); **VE** - Ventura floodplain lake (*n*=231).

Table 1. Mean values of the index of overlap (*Cxy*) trophic groups. (*n* = number of iterations of overlap index). A- Collectorgatherers, B- Collector-filterers, C- Shredders-herbivores, D- Facultative predators.

Trophic groups	A (n=2248)	B (n=272)	C (n=441)	D (n=547)
A. Collector-gatherers	-	-	-	-
B. Collector-filterers	0.64 (0.49-0.75)	-	-	-
C. Shredders- herbivores	0.62 (0.40-0.73)	0.53 (0.31-0.76)	-	-
D. Facultative predators	0.45 (0.12-0.74)	0.47 (0.22-0.81)	0.39 (0.20-0.82)	-

The average values of the index showed a tendency to a partial overlap between predators and other trophic groups.

Considering the average values of the analysis in relation to the type of environment, there was partial overlap of niche among collectors-gatherers and each of the other trophic groups, especially in connection with lakes (Figure 3). This fact can be verified especially between the stations of the floodplain lakes: Patos, Sumida and Finado Raimundo.

All interactions possible and the highest number of total niche overlap (> 0.6) were observed in the Cervo lake, including, besides the abovementioned interactions, among other collector-filterers and shredder-herbivores, predators (Figure 3). The lowest index values were recorded for niche overlap between predators and trophic groups corresponding to collector filterers and shredder-herbivores. There was no niche overlap between trophic groups in Ivinhema River and Jacaré floodplain lake.

The overlap niche of Chironomidae of morphotypes did show significance with nestedness patterns, using the metric T^{10} showed P(T<6.48)=6.17e-64 [-20.08] with

93.5% nesting. The NODF test with significance T= 36.2 e p<0.001 with 63.8% nesting.

There was wide variation between these two extreme groups of generalist and specialist species (Figure 4). Generalist groups exploited the greater number and variety of food items in the environment, with a downward trend in the number of algae species among taxa, *Chironomus streinzkei* and *Stenochironomus*. The amount of food resources characterised groups of generalists to specialists within the food web (Figure 4), namely species richness of algae found in each morphotype Chironomidae.

Among the diatoms, *Aulacoseira granulata* (90%), *Fragilaria* sp.1 (63%) and *Trachelomonas* sp.2 (63%) were the predominant algae in feeding taxa. Fungal spores, Sponge spicules and Algae fragments were items consumed by 77% of the taxa analysed. Plant fragments were consumed by 57%, mainly by *Chironomus streinzkei*, *Aedokritus* sp. (collectors-gatherers), *Polypedilum* (*Tripodura*) and *Stenochironomus* sp. (shredders-herbivores).

In all the studied environments, *Chironomus streinzkei* (Figure 5; 105) fed on 58 algal species, with the greatest variety in the Patos and Cervo floodplain lakes. The greater

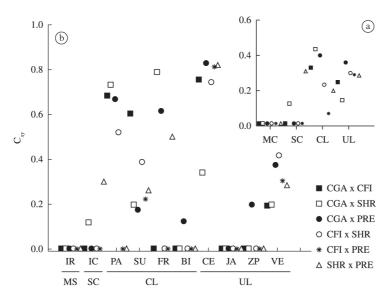


Figure 3. Index of niche overlap (*Cxy*) among trophic groups in four types of environments (a), and during the twelve sampling stations (b). **MC**- main channel, **SC**- secundary channel, **CL**- connected lakes, **UL**- unconnected lakes (a) and the twelve sampling stations (b) - **IR** – Ivinhema River; **IC** – Ipoitã channel; **PA** – Patos floodplain lake; **SU** – Sumida floodplain lake; **FR** - Finado Raimundo floodplain lake; **BI** - Boca do Ipoitã floodplain lake; **CE** - Cervo floodplain lake; **JA** - Jacaré floodplain lake; **ZP** - Zé do Paco floodplain lake; **VE** - Ventura floodplain lake. **CGA**-Collectors gatherers; **CFI** – Collectors filteres; **TRI** – Shredders herbivores; **PRE** – Falcutive predators.

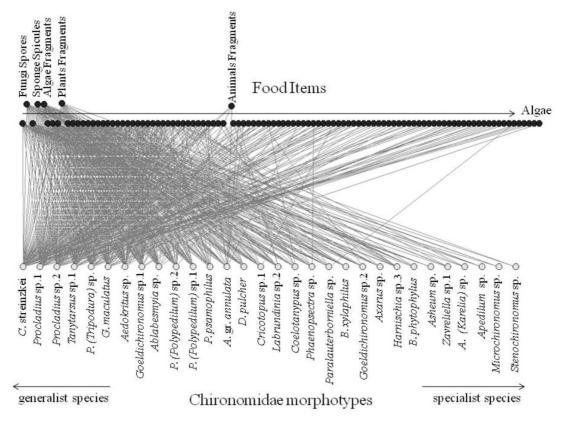
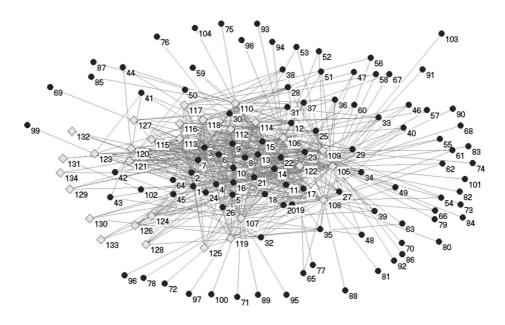


Figure 4. Trophic interaction net of Chironomidae morphotypes (sliver circles) and food resources (black cicles).



Food resources						Chironomidae morphotypes
A. granulata	27	Pinnularia sp.2	53 Amphora sp.	79	Eunotia elegans	105 Chironomus streinzkei
Fungi spores	28	Eunotia bidens	54 Encyonema mesianum	80	Eunotia indica	106 Procladius sp.1
Pinnularia sp.1	29	Eunotia sp. 2	55 Eunotia diodon	81	Eunotia pectinalis	107 Procladius sp.2
Sponge spicules	30	Surirella elegans	56 Eunotia lineolata	82	Eunotia pectinalis	108 Tanytarsus sp.1
Algae fragments	31	Surirella sp.1	57 Eunotia proverrypta	83	Eunotia trigibba	109 Polypedilum (Tripodura)
Fragilaria sp.1	32	Eunotia bilunaris	58 Eunotia serra	84	Fragilaria capuccina	110 Goeldichironomus maculatus
Trachelomonas sp.2	33	Acnanthes sp.1	59 Eunotia trioton	85	Fragilaria quadrata	111 Aedokritus
Gomphonema gracile	34	Surirella linearis	60 Fragilaria lata	86	Fragilaria sp.2	112 Goeldichironomus sp.1
Plants fragments	35	Aulacoseira sp.	61 Fragilaria pinnata	87	Gomphonema sp.1	113 Ablabesmyia sp.
Gomphonema parvulum	36	Cyclotella sp.2	62 Fragilariforma javanicum	88	Gomphonema sp.4	114 Polypedilum (Polypedilum) sp.
Navicula cf. constans	37	Carpatograma cruscicula	63 Gomphonema acuminatum	89	Gomphonema vibrio	115 Polypedilum (Polypedilum) sp.
Cymbella sp.1	38	Eunotia formica	64 Gomphonema augur	90	Luticola multica	116 Pelomus psamophilus
Eunotia sp. 1	39	Encyonema sp.1	65 Gomphonema sp.3	91	Nitzchia sp.	117 Ablabesmyia gr. annulata
Gomphonema sp.2	40	Navicula sp.1	66 Pinnularia subcaptata	92	Pinnularia luculenta	118 Djalmabatista pulcher
Eunotia flexuosa	41	Synedra goulardii	67 Stenopterobia capitata	93	Pinnularia neomajor	119 Cricotopus sp.1
Eunotia inflata	42	Animals fragments	68 Cyclotella meneghiniana	94	Pinnularia transversa	120 Labrundinia sp.2
A. ambigua	43	Eunotia arcus	69 Acnanthes exigua	95	Stauroneis sp.	121 Coelotanypus sp.
Eunotia sp. 4	44	Eunotia jemtlandica	70 Acnanthes sp.2	96	Surirella angusta	122 Phaenopsectra sp.
A. ambigua var. spiralis	45	Eunotia rabenhorstii	71 Caloneis pulchra	97	Surirella robusta	123 Paralauterborniella sp.
Caloneis sp.1	46	Eunotia sp. 3	72 Caloneis sp.2	98	Surirella sp.3	124 Beardius xylaphilus
Pinnularia divergens	47	Eunotia sp. 5	73 Cocconeis sp.	99	Surirella splendida	125 Goeldichironomus sp.2
Trachelomonas sp.1	48	Frustulia rhomboides	74 Cymbella acuta	100	Synedra sp.1	126 Axarus
Aulacoseira alpigena	49	Gomphonema truncatum	75 Cymbella diminuta	101	Trachelomonas oblonga	127 Harnischia sp.3
Cyclotella sp.1	50	Sellaphora pupula	76 Cymbella sp.2	102	Trachelomonas rugulosa	128 Beardius phytophilus
Eunotia papilio	51	Surirella sp.2	77 Encyonema selesianum	103	Trachelomonas scupta	129 Asheum sp
Pinnularia cf. polyonca 52		Acnanthes minutissima	78 Eunomuscicola var. tridentula	104	Trachelomonas sp.3	130 Zavreliella sp.1
						131 Ablabesmyia (Karelia)
						132 Apedilum
						133 Microchironomus sp.
						134 Stenochironomus sp.

Figure 5. Networks by Chironomidae morphotypes (*silvers diamonds*) and food resources (*black circles*). The codes (numbers) are in Table 1.

number of animals fragments was found in pet digestive content of the predator *Procladius* sp. (106), mainly in the Patos floodplain lake.

Asheum sp. (129), Zavreliella sp.1 (130), Ablabesmyia (Karelia) (131), Apedilum sp. (132), Microchironomus sp. (133) and Stenochironomus sp. (134) were the taxa with the smallest variety of algal species recorded in digestive contents, with only one representative of each algae species by taxon (Figure 5). Larvae Microchironomus

sp. Particularly exploited sponge spicules in the Zé do Paco floodplain lake, and *Stenochironomus* sp. fuelled especially plants fragments in the Ipoitã channel and Ventura floodplain lake.

4. Discussion

The low or absence of niche overlap in Ivinhema River and unconnected floodplain lakes like Jacaré and Zé do Paco were probably due to the fact that the Ivinhema River has greater flow of water with constant introduction or removal of food available for the larvae. When low stability of habitat occurs, this leads to small quantities of food resources available thereby reducing the richness and density of Chironomidae taxa in these environments.

In unconnected floodplain lakes, the low densities of Chironomidae larvae were due to these lentic environment having great input of organic matter from allochthonous sources and the start of the decomposition process that causes low oxygen of water, consequently selecting tolerant species.

Liu and Wang (2008), in studies on unconnected floodplain lakes and rivers in China, concluded the effect of current on benthic fauna reduced the overlap between trophic groups. Probably, in the studied area food resources for larvae were less available in channels than floodplain lakes.

The connected floodplain lakes had the highest number of niche overlap in relation to other types of environments, probably related to interactions of the most abundant taxa especially collector-gatherers as *Aedokritus* sp. and *Chironomus streinzkei* exploiting a greater number of food items than the other taxa.

Studies of Zilli et al. (2008) verified in the Medium Paraná River the trophic group (collector-gatherers) as more abundant, especially the species *Chironomus streinzkei* which also predominated in unconnected floodplain lakes. Therefore these species are typical of these environments and have the same feeding strategy making these larvae and their niches overlap, and also ending overlap niches of other trophic groups.

In floodplain lakes there is the presence of macrophytes that provide development of a higher number of interactions between Chironomidae larvae. Such interactions cause overlap and its resulting development of many adaptations, between taxa of the same groups and of different trophic groups (Schmid and Schmid-Araya, 1997).

However, the overlap niches do not necessarily reflect competition between species, but coexistence with a partial overlap of potential niches, as observed by low index values overlap between predators and other trophic groups.

The results demonstrated that trophic interaction is standard nesting in the overlap niche of Chironomidae larvae. This pattern of nesting is shown as nested in the morphospecies niches and the variety of features allows the coexistence of these morphospecies often in the same environments; the same result was verified by Galizzi et al. (2012). Therefore, environments that foster the diversity of these resources will facilitate the coexistence of these morphospecies thus increasing local diversity.

Species that have high values of food items occurred in diverse environments as generalists, and great overlap niche and those with few food items with less overlap niche were classified as specialists. *C. streinzkei, Procladius* sp.1, *Procladius* sp.2, *Tanytarusus* sp.1, *Polypedilum (Tripodura)* sp. and *Goeldichironomus* sp.1 can be considered as the main generalist species of 30 Chironomidae larvae while *Beardius* sp.1, *Asheum* sp., *Zavrelliella* sp.1, *Ablasbemyia*

(*Karelia*) sp., *Apedilum* sp., *Microchironumus* sp. and *Stenochironomus* sp. can be considered as specialist species, showing a pattern of nested overlap.

Species from the centre region are more likely to be generalists with a wide niche breadth and marginal species are more likely to be specialists (Heino and Soininen, 2006), but this may not apply to all species found in our centre region.

We conclude that the natural conditions and food availability may determine how the organisms in aquatic environments can colonise different habitats or migrate. Food items among different groups can generate strong trophic interactions for space and food, and may facilitate the coexistence of species of predators and collector-gather groups by food availability and space. The consumption of diatoms was not restricted to organisms typically considered herbivores. A large supply of decaying debris that serves as a food source confers some benefits to organisations that can colonise rapidly connected floodplain lakes.

The study showed the majority of larvae are generalist and highly opportunistic feeding on algae and detritus and possibly of other Chironomidae larvae, and spatial distribution in patches varied according to the type of environment and the species can coexist due to the wide variety of food resources, mainly algae.

In conclusion, this study contributes to the understanding of relationships and trophic niche and overlap of Chironomidae, it turn contributing to the understanding of larvae ecology providing a base for ecological studies of aquatic insects in Neotropical floodplain environments.

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